

PARENTAL FEEDING OF NESTLING NASHVILLE WARBLERS: THE EFFECTS OF FOOD TYPE, BROOD-SIZE, NESTLING AGE, AND TIME OF DAY

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About 90% of all bird species are reportedly monogamous (Wittenberger 1982). Monogamous mating systems are associated with biparental care, and one hypothesis for the evolution of such mating systems is that male help is essential to the successful rearing of young. A prediction of this hypothesis is that a male should contribute a substantial amount of food to the raising of nestlings; this was tested in an essentially monomorphic, monogamous paruline, the Nashville Warbler (*Vermivora ruficapilla*).

Relative parental contribution in terms of rates of feeding young can be influenced by demands of the nestlings (e.g., brood-size, nestling age) and/or by environmental factors (e.g., weather conditions, time of day, time of season) (Royama 1966, Willson 1966, Seel 1969, Best 1977, Pinkowski 1978, Johnson and Best 1982, Wittenberger 1982, Bédard and Meunier 1983). Rates of feeding per se can be potentially misleading in determining relative contributions of the male and female parent if the food packages brought to the young differ in some way between the parents; a few studies (e.g., Howe 1979, Knapton 1980, Johnson and Best 1982, Biermann and Sealy 1982, Bédard and Meunier 1983, Knapton and Falls 1983) have taken this into account in their comparisons of male and female contributions.

The objectives of this study were: (1) to document patterns of feeding nestling Nashville Warblers between members of a pair; and (2) to compare these patterns between pair members as they relate to brood-size, nestling age, and time of day. In the comparisons, I take into account not only rates of feeding but also the identity, size, and number of prey items.

METHODS

The study was carried out in Algonquin Provincial Park, Ontario, during the breeding seasons of 1981 and 1982. The habitat occupied by Nashville Warblers in the park is mixed coniferous and deciduous woodland with open areas covered with low shrubs (primarily *Vaccinium* spp.), ferns and forbs.

We located nests by systematically searching openings in the forest in three study areas. All nests were discovered when the incubating bird (in all instances, the female) was flushed from the nest. All nests when found contained eggs, and a daily log of each nest's progress was kept until it was empty, either the young fledged or the nest contents depredated. Thus, the age of the nestlings at any given time could be determined.

Adults were caught in two ways: (1) in mist nets with a playback of a Nashville Warbler's song; and (2) by butterfly net, a method which proved most effective in catching the incubating female (Knapton, unpubl.). This latter method involved approaching the nest and quickly covering it with the net. Most birds were caught on the first attempt, no bird sustained an injury from this method, and no nest was lost to desertion. Each bird caught was color-banded, for individual recognition, and sexed by presence or absence of cloacal protuberance and by slight plumage differences (females tended to be slightly duller than males). Subsequent behavioral differences (e.g., singing by males, incubating by females) confirmed these sexing methods.

Nashville Warbler nests were watched from blinds set up about 10 m away, and the parent birds were observed as they approached the nest with food in their bills, fed the nestlings, and then flew off (called a feeding trip). Most nests were watched on 5 consecutive days, from day 4–day 8 of the nestling period (the young fledged on day 9), in the period 11–26 June. Observation periods were about 3 h long, and were carried out between 08:00 and 20:00 EDT. For analysis, each day was divided into four 3-h time periods: 08:00–11:00, 11:00–14:00, 14:00–17:00, and 17:00–20:00. No observations were carried out in cool or rainy weather. Pairs appeared to accept the presence of blinds, and no nest under observation was deserted. Information was recorded on portable tape recorders and later transcribed.

From blinds, the following information was recorded: (1) the number of foraging trips; (2) the sex of the bird making the trip; (3) the number of prey items each bird brought back to the nest at each trip; (4) where possible, the identity of the prey items, at least to order and occasionally to family; and (5) the size of each prey item, to the nearest 0.5 cm, relative to bill length (8–10 mm).

In 1980, nestlings from five nests (two nests of three young, two of four young, one of five young) were weighed to the nearest 0.1 g from day 0 (day of hatching) to day 8, and growth curves constructed (Knapton and Cartar, unpubl.). Analyses of variance showed no significant differences in nestling weight at any age among different brood-sizes. Young were not weighed in 1981 and 1982 to avoid disruption of nesting activity and possible increased predation levels from observer activity.

Data were analyzed by one-way or two-way ANOVAs, or by paired *t*-tests. The degree of dietary overlap between males and females was determined using Horn's (1966) measure of overlap, *C*, given by the equation:

$$C = \frac{2 \sum_{i=1}^s X_i Y_i}{\sum_{i=1}^s X_i^2 + \sum_{i=1}^s Y_i^2}$$

where X_i and Y_i are the proportions of prey species *i* for males and females, respectively. A value of 0% means no overlap, a value of 100% means total overlap.

RESULTS

Eleven nests were watched, at an average of 16.4 h/nest; 1324 foraging trips were recorded. Five nests were observed in 1981 and six in 1982; there were no differences in feeding rates between years for males ($t = 0.46$, NS) or for females ($t = 0.64$, NS), hence data for both years were pooled. Brood-size was four nestlings in six nests and five nestlings in five nests.

TABLE 1
A COMPARISON OF INTERSEXUAL FEEDING RATES IN 11 PAIRS OF NASHVILLE WARBLERS

Pair	Feeding rates (trips/h)			Brood-size
	Male	Female	Total*	
1	5.88	5.06	10.94	4
2	1.45	8.84	10.29	5
3	4.60	4.07	8.67	5
4	4.16	4.45	8.61	4
5	4.01	3.67	7.68	5
6	3.53	3.60	7.13	4
7	2.94	3.96	6.90	4
8	3.49	3.39	6.88	5
9	2.91	2.95	5.86	5
10	2.72	3.01	5.73	4
11	0	3.43	3.43	4

* Total feeding rates are arranged in decreasing frequency.

Comparison of total male and female contributions to feeding nestlings.—There was no difference between the sexes in feeding rate (Table 1: $t = 1.35$, $df = 10$, NS). Mean male feeding rate was 3.24 ± 1.57 trips/h, and mean female feeding rate was 4.22 ± 1.65 trips/h. The lower mean rate of feeding by males is almost entirely due to two nests at which the female contributed much more than her partner, at 85.9% at nest 2 and 100% at nest 11. At the nine other nests, males and females contributed more or less equally (Table 1: $t = 0.21$, $df = 8$, NS). The absence of male feeding trips at nest 11 was not because the male was not present: the male made frequent visits to the vicinity of the nest but never with food in its bill and never actually to the nest itself.

Number, size, and identity of prey delivered to young.—Number of prey items per foraging trip ranged from one to three (males: $\bar{x} = 2.01 \pm 0.51$; females: $\bar{x} = 1.78 \pm 0.34$). There was no difference between the sexes in number of prey brought to the nest; mean number of prey delivered to nestlings/h for males was 6.51 ± 1.48 and for females was 7.52 ± 1.28 ($t = 1.06$, $df = 10$, NS).

Prey type did not differ between the sexes; the dietary overlap value $C = 94\%$, indicating almost complete overlap between males and females in prey type. Lepidoptera larvae comprised 89% of all prey types, the remaining 11% being made up of adult Diptera, spiders, adult Coleoptera, and an unidentified category. Lepidoptera larvae comprised 88% of male contributions and 90% of female contributions.

Prey length also did not differ between the sexes ($F = 0.94$, $df = 1,60$,

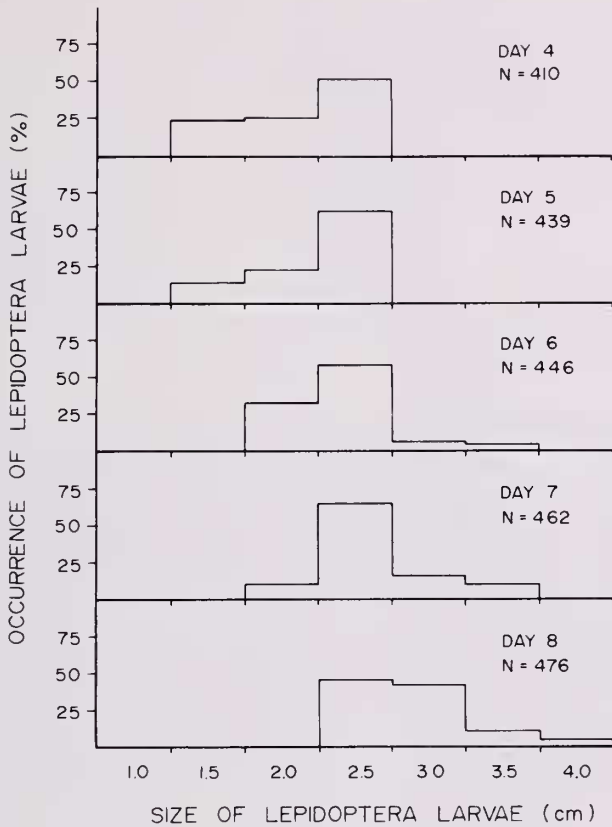


FIG. 1. Frequency distribution of Lepidoptera larvae of different sizes as a function of nestling age. N = total number of larvae per each age class.

NS). The most frequent size of Lepidoptera larvae taken was 2.5 cm long, followed in decreasing frequency by larvae at 2, 3, 1.5, 3.5, and 4 cm long, respectively (Fig. 1). However, prey size did increase with age of nestlings (see below). As a general conclusion, there was no difference between males and females in number, prey type, or size of prey delivered to nestlings.

Brood-size.—Brood-size did not affect feeding frequency ($F = 0.27$, $df = 1, 18$, NS), and there was no brood \times sex interaction ($F = 0.17$, $df = 1, 18$, NS). Mean rates of nest visitation were as follows: males = 3.21 ± 1.94 for broods of four, and 3.28 ± 1.20 for broods of five; females = 3.92 ± 0.74 for broods of four and 4.59 ± 2.41 for broods of five.

Brood-size also did not affect feeding frequency in terms of number of

TABLE 2
 MALE AND FEMALE FEEDING RATES (TRIPS/H) AND AGE OF NESTLINGS AT 11 NASHVILLE
 WARBLER NESTS

Age of nestlings (days)	Male ($\bar{x} \pm SD$)	Female ($\bar{x} \pm SD$)
4	2.82 \pm 1.70	4.10 \pm 2.71
5	3.21 \pm 1.45	4.18 \pm 1.50
6	3.38 \pm 1.53	4.13 \pm 1.18
7	3.27 \pm 1.77	4.52 \pm 2.47
8	3.39 \pm 1.99	4.62 \pm 1.96

feeding trips per nestling ($F = 0.41$, $df = 1,18$, NS) and once again there was no brood \times sex interaction ($F = 0.07$, $df = 1,18$, NS).

Nestling age.—Feeding rates of either sex did not change with nestling age (males: $F = 0.73$, and females: $F = 0.51$, for each analysis, $df = 4,50$, NS). Feeding rates remained essentially constant over the 5-day period for both sexes (Table 2), with females averaging more feeding trips/h than males at each nestling age.

There was, however, an increase in prey size with nestling age (Fig. 1; $F = 14.24$, $df = 5,20$, $P < 0.001$). Lepidoptera larvae at 2.5 cm long predominated at all nestling ages, but nestlings at days 4 and 5 received proportionately more larvae 1.5 and 2 cm long; whereas, older nestlings received an increasing proportion of larvae 3–4 cm long. The increase in prey size with nestling age is probably not due to prey availability, as nestling age among nests was not synchronous. There was considerable overlap in nestling age among nests that were watched such that two nests observed on the same day could hold young at any age between 4 and 8 days old.

Time of day.—Time of day had a significant effect on feeding rates (Fig. 2, $F = 4.58$, $df = 3,80$, $P < 0.01$). Most feedings occurred in the early morning and evening periods for both sexes. A comparison of male and female feeding rates during the day showed a significant difference between the sexes (Fig. 2; $F = 7.35$, $df = 1,80$, $P < 0.01$). A general statement is that males fed comparatively less in the early morning and evening periods and more during the rest of the day than females.

DISCUSSION

Relative parental contribution is a function of feeding rates, number of prey items per feeding trip, and nature of the prey. Feeding rates per se are not necessarily a true indicator of parental contribution if aspects

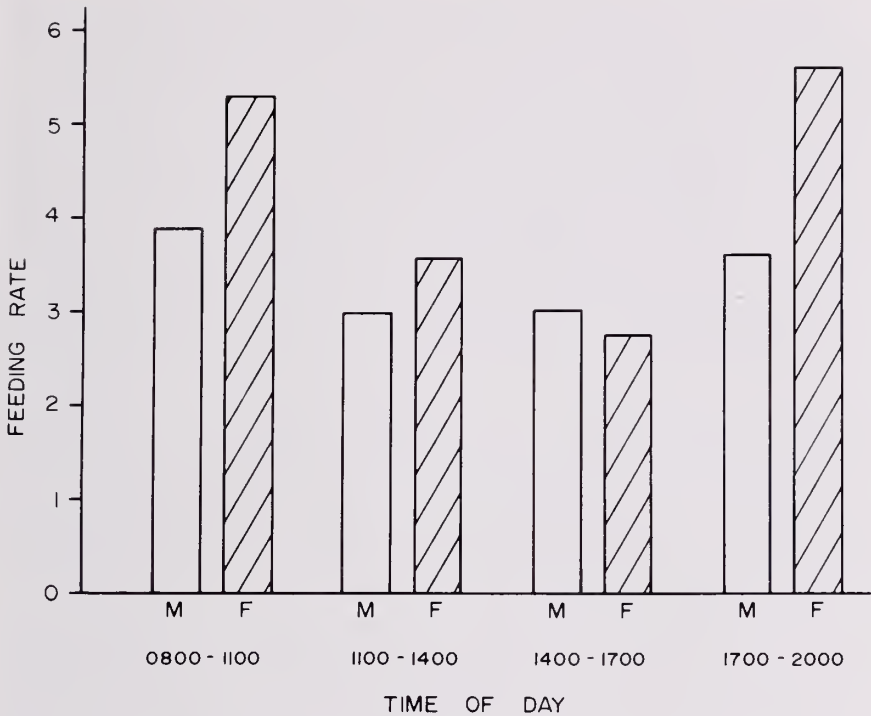


FIG. 2. Comparison of male and female feeding rate (trips/h) according to time of day.

of the prey brought in during feeding trips differ between the sexes (Royama 1966, Howe 1979, Johnson and Best 1982, Wittenberger 1982, Biermann and Sealy 1982, Bédard and Meunier 1983).

In the Nashville Warbler, the nature of the prey (its size and identity) brought to nestlings did not differ between males and females within a pair at each of the 11 nests observed. Lepidoptera larvae were the most common prey item, with larvae 2.5 cm long being the most frequently delivered size. Number of prey items per feeding trip also did not differ between the sexes, either with brood-size or age of nestlings. Males have been found to bring larger food loads in Yellow Warbler (*Dendroica petechia*) at broods of five, but not at broods of three or four (Biermann and Sealy 1982) and in Savannah Sparrows (*Passerculus sandwichensis*) at days 5 and 6 of nestling age, but not earlier or later (Bédard and Meunier 1983). In the Nashville Warbler, there were no differences between sexes for broods of four or five between the ages of 4 and 8 days.

Males and females within a pair contributed essentially equal amounts of food to nestlings in 9 of 11 pairs observed. Total feeding rates did not differ between the sexes at nine nests, which supports the initial prediction, that in an essentially monomorphic, monogamous passerine with biparental care, each member of the pair should contribute substantially to the rearing of young. Interestingly, at the two nests showing strongly skewed parental contributions, it was the male that contributed very little (only 14% at one nest and nothing at the other). Roth (1977) also reported a complete absence of male help at a Nashville Warbler nest. This lack of male assistance was not related to brood-size (Table 1) or to season (June), or to apparent influence of the blind (the male at nest 11 visited the nest area, within 50 cm of the nest, but not the nest and never with food). The female appeared to compensate for low male help at nest 2; the female's feeding rate at 8.84 was the highest of any individual bird (Table 1), but the rate of feeding of the female at nest 11, where there was no male assistance, was not different from rates of females with equivalent male assistance. Young fledged from both nests, but because their fledging weights were not taken, it is not known if young from nest 11 fledged at a lower weight than young from other nests.

Although a linear relationship between feeding frequency and nestling age has been shown to occur in several passerines (e.g., Howe 1979, Pinkowski 1978), most of the increase actually occurs early in the nesting period (Johnson and Best 1982). In Nashville Warblers, such an increase probably occurs before the nestlings reach 4 days of age; in this study, I show that from 4 days to the day before the young fledge, there is no corresponding increase in feeding rate. The increasing energetic demands of the young are met by the adults bringing in larger prey items as a function of nestling age; there was a significant increase in length of Lepidoptera larvae with increase in nestling age (Fig. 1). Some studies (e.g., Royama 1966, Morehouse and Brewer 1968, Biermann and Sealy 1982) have reported an inverse correlation between feeding rate and size of prey items. In the Nashville Warbler, no such inverse correlation was observed, a finding consistent with that in another paruline, the Prairie Warbler (*Dendroica discolor*) (Nolan 1978).

An increase in feeding rate with increasing brood-size has been found in some passerines (Royama 1966, Morehouse and Brewer 1968, Hussell 1972, Best 1977, Johnson and Best 1982) but not in others (e.g., House Sparrow [*Passer domesticus*], Seel 1969; Eastern Bluebird [*Sialia sialis*], Pinkowski 1978; Savannah Sparrow, Bédard and Meunier 1983). In the Nashville Warbler, I detected no relation between feeding rate and brood-size in broods of four or five young. Such correlations (or lack thereof) are probably due to a trade-off between food requirements/nestling and

thermoregulatory costs/nestling (i.e., larger broods have a lower heat loss/nestling owing to a lower surface-to-volume ratio).

Although total feeding rates between males and females did not differ significantly, there were significant differences in feeding rates among time periods within a day, and the proportion of diurnal feedings within a sex differed between sexes. Compared to females, males contributed proportionately less in the early morning and in the evening, and more during the late morning and afternoon periods. This difference is possibly a result of different diurnal behavioral patterns of the sexes; during the early morning and evening, males sing, whereas during the mid-day period females brood the young. The lowest brooding time period is between 18:00–21:00 (Roth 1977), which corresponds closely with the highest feeding rate of the female (Fig. 2).

Thus, these results show that both sexes contribute substantially to the feeding of nestlings and that there is no significant difference between males and females in level of contribution (at least, in 9 of 11 nests observed). The nature of the prey did not differ between the sexes, nor did number of prey per feeding trip. Feeding rates were not influenced by brood-size (for broods of four or five) or by age of nestlings (between 4 and 8 days of age), and the increasing energetic demands of the maturing young were met by the adults bringing in larger prey items as the nestlings grew older. Time of day influenced feeding rates, and a proportional difference between the sexes in diurnal feeding rates is probably due to different behavior patterns of males and females within a day.

SUMMARY

Male and female contributions to feeding nestlings were investigated in an essentially monomorphic, monogamous passerine, the Nashville Warbler (*Vermivora ruficapilla*), for two summers in Algonquin Provincial Park, Ontario. The identity, size, and number of prey items per feeding trip did not differ between the sexes. In general, feeding rates were not significantly different between males and females and were not influenced by brood-size between broods of four or five young. Males and females made equal contributions to feeding nestlings, as predicted from mating system theory, at 9 of 11 nests. At the remaining two nests, one male contributed very little (14%), and the other male contributed no food at all.

The number of feeding trips was not influenced by age of nestlings; however, the adults brought in larger prey items as the nestlings grew older to meet the increasing energetic demands of the maturing young. Time of day influenced feeding rates (the highest rates were in the early morning and evening), and the proportion of diurnal feedings within a sex differed between the sexes, probably reflecting a difference in diurnal behavior patterns between males (singing behavior) and females (brooding).

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